

Soil ecology and ecosystem services of dairy and semi-natural grasslands on peat

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ABSTRACT

Peat wetlands are of major importance for ecosystem services such as carbon storage, water regulation and maintenance of biodiversity. However, peat drainage for farming leads to CO₂ emission, soil subsidence and biodiversity losses. In the peat areas in the Netherlands, solutions are sought in reducing drainage, adapting farming to wetter soils, and converting productive dairy grasslands to less intensively managed semi-natural grasslands. Our objective was to compare the soil ecology and related ecosystem services of dairy and semi-natural grasslands on peat soils (Terric Histosols). Soil biotic and abiotic parameters were measured in twenty dairy and twenty semi-natural sites, with particular focus on (i) soil faunal diversity (ecosystem service “maintenance of biodiversity”), (ii) CO₂ emission (“climate regulation”), (iii) water infiltration (“water regulation”) and (iv) soil fertility (“grass production”). Mean soil faunal taxonomic richness per site (alpha diversity) was higher in dairy grasslands compared to semi-natural grasslands. However, the total observed number of taxa (gamma diversity) in dairy grassland was 13% lower for soil fauna and 21% lower when including plant species. Potential C mineralization rate in the topsoil – used as a proxy for CO₂ emission – was not influenced by land use but was limited by drought. Additionally, potential C mineralization depended on different C sources and microbial groups in the two grassland types. Water infiltration rate differed by a factor of five between land use types (dairy > semi-natural), and correlated with soil porosity. As expected, soil fertility was higher in dairy than in semi-natural grasslands. However, potential N mineralization was similar in dairy and semi-natural grasslands and was correlated negatively with bacterial biomass apparently indicating N immobilization, and positively with bacterial growth that depended on labile C and N in soil. Our study on peat soils shows that dairy versus semi-natural grassland use influences biodiversity, climate regulation, water regulation and (potential for) grassland production. We conclude with recommendations for land management to optimize the delivery of those ecosystem services.

1. Introduction

Peat wetlands worldwide deliver important ecosystem services such as carbon (C) storage, maintenance of biodiversity and water regulation (Maltby and Immirzi, 1993; Verhoeven and Setter, 2010). In the river deltas of the Netherlands, land reclamation for agriculture by peat drainage and peat harvesting for fuel was carried out from the Middle Ages onwards (Van de Ven, 1993) and caused soil subsidence, resulting in a decline of peat-covered land area. At present, 8% of the surface of

the Netherlands is covered by peat soil and is in use for grassland based dairy farming (82%), semi-natural grasslands (7%), nature (5%), and infrastructure, buildings and surface water (De Vries, 2004; Van den Born et al., 2016). For productive dairy grasslands, the ground water level is kept well below the soil surface (generally 30–70 cm) by drainage. A major drawback of this land use is net decomposition of organic matter in the oxic topsoil, resulting in carbon dioxide (CO₂) emission (Kasimir-Klemedtsson et al., 1997; Van den Akker et al., 2008), soil subsidence (Schothorst, 1977) and high infrastructural costs (Van den

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Born et al., 2016). Moreover, additional issues related to dairy grasslands on drained peat have been reported: loss of floral and faunal aboveground biodiversity, including meadow birds (Beintema, 1986; Lamers et al., 2002), and eutrophication (Bobbink et al., 1998).

These observations, together with (inter)national agendas on biodiversity and climate, lead to increasing pressure from society on agricultural peat areas to maintain biodiversity, reduce CO₂ emission and provide water storage capacity (Van den Born et al., 2016). Thus, peatlands are challenged to deliver not only provisioning but also regulating and supporting ecosystem services (MEA, 2005). Solutions are seen in increasing the area of (semi-) natural grasslands and natural peat vegetation at higher ground water level, or in “nature-inclusive” agriculture with reduced drainage intensity, use of submerged tile drains and adaptation to wetter soils (Erisman et al., 2016; Van den Akker et al., 2008; Van den Born et al., 2016). Such changes should result in delivery of ecosystem services closer to the societal needs. For policy choices on land management in accordance with these needs, it is necessary to know how the delivery of ecosystem services changes following land use and land management changes. Dutch peatland has been drained intensively for centuries, and hence, the implications constitute a valuable case study for the development of sustainable use of peat soils in both the Netherlands and other countries.

Differences between peat grasslands managed for dairy production or for nature restoration have been studied in the Netherlands in relation to specific ecosystem components or processes, such as floral diversity (Berendse et al., 1992; Van Dijk et al., 2007), meadow birds (Schekkerman and Beintema, 2007; Verhulst et al., 2007), or soil biology, soil chemistry and peat decomposition (Brouns et al., 2016; Van de Riet et al., 2013; Van Dijk et al., 2009). However, because of the variety in delivery of ecosystem services with possible trade-offs, there is a need for integral knowledge across different land uses (Breure et al., 2005). Within the peat area, the monitoring programme of the Dutch Soil Quality Network covered only the land use “dairy farming”, and did not include comparisons with other land use types (Rutgers et al., 2009). The objective of this paper is therefore to provide a comparison of the soil ecology and the related provision of ecosystem services of peat grasslands either used for grass production (“dairy grasslands”) or for nature restoration and conservation (“semi-natural grasslands”).

We selected dairy and semi-natural grasslands on peat (27–65% organic matter) and measured soil biotic and abiotic parameters, and botanical composition. To limit the influence of site-specific properties twenty replicates (grasslands) per land use type were sampled. Also, to minimize short-term effects of nutrient and C inputs to the soil, measurements were carried out during spring, before application of manure. In the interpretation we focus on the following parameters and ecosystem services: (i) soil faunal diversity (ecosystem service “maintenance of biodiversity”), (ii) CO₂ emission (“climate regulation”), (iii) water infiltration (“water regulation”) and (iv) soil fertility (“grass production”). We hypothesize that the higher nutrient input in dairy grasslands leads to soil faunal communities with a lower taxonomic richness. In addition, we hypothesize that dairy grassland soils have higher microbial activity and CO₂ emission due to higher C inputs (plant residues, cattle manure) and more oxic conditions, but have less crumb structures and lower water infiltration rates than semi-natural grasslands due to compaction by machinery and livestock. Finally, we expect dairy grassland soils to have higher pH, contain more plant available nutrients and have higher potential N mineralization than semi-natural grasslands.

2. Materials and methods

2.1. Study sites

In the western peat district of the Netherlands, we selected twenty replicates for each grassland type studied: on commercial dairy farms (“dairy grasslands”) and in areas owned and managed by nature

Table 1

Management and plant parameters of dairy (n = 20) and semi-natural (n = 20) grasslands on peat (means, standard deviations, *P*-values). Plant species in Supplementary Table S1.

Parameter	Unit	Dairy		Semi-natural		<i>P</i> -value
		mean	s.d.	mean	s.d.	
<i>Historical management</i>						
Ditch water level (summer)	cm below soil surface	49	8	40	14	0.009
N from organic manure	kg N ha ⁻¹ yr ⁻¹	216	55	43	50	< 0.001
N from mineral fertilizer	kg N ha ⁻¹ yr ⁻¹	140	91	0	0	< 0.001
Number of grass cuts	n yr ⁻¹	2.7	0.8	1.1	0.5	< 0.001
<i>Botanical composition</i>						
Monocotyledon soil cover	%	82.5	10.6	55.1	21.1	< 0.001
Dicotyledon soil cover	%	8.8	10.0	22.6	16.2	0.002
Number of plant species	n	15.2	3.2	14.8	5.3	0.104

conservation organizations (“semi-natural grasslands”). Selection criteria were: (i) situated on peat soil (Terric Histosol; FAO, 2015) (ii) minimum sward age of ten years, (iii) summer ditch water level within the range of 20–60 cm below soil surface and (iv) no major changes in management (drainage, fertilization, stocking) in the past five years. At each site, an experimental plot (6 m × 9 m) was laid out. During the experimental year, the plots remained unfertilized, ungrazed and unmown until soil sampling.

The dairy grasslands had an average ditch water level (summer) of 49 cm below soil surface (Table 1), ranging from 30 to 60 cm, and a conventional management with a history of mixed grazing and cutting. The year before the measurements, the dairy grasslands received on average 140 kg N ha⁻¹ as inorganic fertilizer and 216 kg N-total ha⁻¹ as cattle manure (mainly slurry manure; excluding excretion during grazing).

In the semi-natural grasslands, mean ditch water level was 40 cm below soil surface (range 20–60 cm), significantly higher than in dairy grasslands (*P* < 0.01; Table 1). Most of the semi-natural grasslands were extensively grazed by sheep or young cattle, cut once or twice a year after the chick season of meadow birds and had a low manure input of on average 43 kg N-total ha⁻¹ yr⁻¹, mainly as solid cattle manure (excluding excretion during grazing). Three grasslands were not manured nor grazed, but mown once a year to keep the vegetation open and to export nutrients.

2.2. Vegetation survey

Botanical composition was measured in June 2010 according to the Braun-Blanquet cover-abundance method (Westhoff and van der Maarel, 1978). Before statistical analyses, Braun-Blanquet scores were replaced with a fully numerical 1–9 scale (Van der Maarel, 1979).

2.3. Soil measurements

All soil sampling and *in situ* measurements were carried out between 20 and 28 April 2010. In each plot, a bulk sample consisting of c. 50 randomly taken soil cores (0–10 cm, ø 2.3 cm) was collected. This sample was sieved through 1 cm mesh, homogenized and split into subsamples for biotic (nematodes, microbes and microbial processes) and abiotic (chemical composition, particle size distribution and gravimetric water content) analysis. Separate samples were taken for soil meso- and macrofauna and additional soil physical and chemical measurements.

2.3.1. Soil biological measurements

Fungal biomass, bacterial biomass, bacterial growth rate ($[^3\text{H}]$ thymidine and $[^{14}\text{C}]$ leucine incorporation into bacterial DNA and proteins), potential C mineralization and potential N mineralization were determined for each site as described in Van Eekeren et al. (2010), except that samples were incubated at field-moisture content.

Nematodes, enchytraeids, earthworms and microarthropods were sampled and determined for each site as described in Van Eekeren et al. (2010). Additionally, nematode channel index, enrichment index and structure index (Ferris et al., 2001) were calculated with the relative abundance data using NINJA (Sieriebriennikov et al., 2014). For earthworms, the number of species per plot was corrected for small sample size with Fischer's alpha diversity index (Fisher et al., 1943). Microarthropods were counted, identified to species and assigned to feeding guilds.

Diversity and abundance indices were calculated. The Shannon species diversity index (H) (Shannon, 1948) was calculated separately for each soil faunal group and experimental plot. Furthermore, we calculated one combined soil faunal taxonomic richness index for the groups together, per plot. The number of taxa was first standardized per group by subtracting the mean and dividing by the standard deviation ($n = 40$), resulting in a range of values with mean = 0 and standard deviation = 1 (Wagg et al., 2014). These standardized values were then divided by four (i.e. the number of faunal groups) and summed up to a single "combined soil faunal taxonomic richness index" with mean = 0. The same procedure was used for a "combined soil faunal abundance index".

2.3.2. Soil physical measurements

In each plot, five undisturbed 100 cm³ soil cores were taken in the 5–10 cm soil layer. Bulk density, water content at water saturation and at pF 2.0 were determined using the ISO11274 method. Air content at pF 2.0 was calculated from the weight difference between samples at pF 2.0 and water-saturated samples. Actual soil water content was determined in the 0–10 cm bulk sample by drying two 30 g sub-samples at 105 °C to constant weight.

Soil penetration resistance was measured using an electronic penetrometer (Eijkkelkamp, Giesbeek, The Netherlands) with 2.0 cm² penetration surface and a 60° apex angle. Cone resistance was recorded per cm of soil depth and expressed as the average of 10 penetrations per layer (0–10, 10–20 and 20–30 cm). Load bearing capacity was measured at 10 randomly chosen spots in each plot using a penetrometer (5.0 cm² penetration surface, 60° apex angle), and expressed as the maximum force (N) needed to push the cone through the sod.

Soil particle size distribution was measured in 2 g sub-samples of the 0–10 cm bulk sample as described in Van Eekeren et al. (2010). Clay and silt percentages were corrected according to Buurman et al. (2001) for underestimation (clay) and overestimation (silt) by the laser diffraction method compared to the pipette method. Finally, values were recalculated to percentage of total soil weight including organic matter.

Soil structure in the 0–10 and 10–20 cm layers (distribution of crumbs, sub-angular and angular elements, and density of macropores and roots) and water infiltration rate into the soil were measured *in situ* as described in Van Eekeren et al. (2010).

2.3.3. Soil chemical measurements

For each site, soil from the 0–10 cm bulk sample was oven-dried at 40 °C prior to analysis of acidity (pH_{KCl}), organic matter (SOM), total carbon (C_{total}), total nitrogen (N_{total}), total phosphorus (P_{total}) and ammonium-lactate-extractable P (P_{AL}), as described in Van Eekeren et al. (2010).

Water soluble carbon (WSC) and hot water extractable carbon (HWC) were analyzed according to Ghani et al. (2003). Field-moist soil from the 0–10 cm bulk sample was extracted with 30 ml distilled water for 30 min, centrifuged for 20 min and filtered. The filtrate was used to measure WSC. Next, the sediments in the centrifuge tubes were shaken

with a fresh amount of 30 ml distilled water for 10 s and left for 16 h in a hot-water bath at 80 °C. After filtration, the filtrate was used to measure HWC. Both HWC and WSC were expressed per g dry soil.

Potentially mineralizable N was determined by anaerobic incubation of 16 g of soil from the 0–10 cm bulk sample as described in Van Eekeren et al. (2010).

Finally, soil samples from the 0 to 20 cm layer were analyzed for cation exchange capacity (CEC), Ca, Mg and K saturation, and nitrate concentration with a Mehlich 3 extractant by Soil Tech Solutions (www.soiltech.nl).

2.4. Statistical analyses

The measurements yielded a database with 147 soil parameters measured in forty sites. Where necessary, parameter values were log-transformed to obtain a normal distribution.

First statistical analyses were carried out in Genstat (18th edition, VSN international, UK). For each parameter, we tested for the effect of land use ("dairy" versus "semi-natural") by one-way ANOVA. Control of false positive results due to the large number of parameters tested was done according to Benjamini and Hochberg (1995) with the total list of P -values from the ANOVAs. For the whole group of tests, maximum P -value for a difference in an individual parameter was 0.024 at $\alpha = 5\%$ (significant difference), and 0.056 at $\alpha = 10\%$ (trend). When correlations between parameters were expected, Pearson sample correlations and their significances were determined.

Additionally, structural equation modeling (SEM) was carried out in R with the lavaan package (Rosseel, 2012). SEM was used to improve our mechanistic understanding by finding determinant (explanatory) soil quality factors for the following dependent parameters: (i) combined index of soil faunal taxonomic richness, (ii) potential C mineralization, (iii) water infiltration, and (iv) potential N mineralization. For each dependent parameter we started with a hypothesis model, built with explanatory parameters and pathways based on our knowledge of soil processes. We then improved and simplified the initial model by adding omitted significant pathways based on the modification index (mi) and by excluding non-significant pathways ($P > 0.05$). The quality of the total models was assessed using the Chi² statistic, the root mean square error of approximation value (RMSEA) and the Akaike information criteria (AIC) (Kline, 2015). An adjusted Chi²-square probability was calculated with the Monte Carlo MCX2 function to correct for the limited sample size ($n = 40$) (Shipley, 2016).

3. Results

3.1. Botanical composition

Monocotyledons were dominant in both dairy and semi-natural grasslands (Table 1). Dairy grasslands had a higher soil cover of monocotyledons and a lower cover of dicotyledons than semi-natural grasslands. The most common plant species were *Lolium perenne* L., *Poa trivialis* L. and *Poa pratensis* L. in dairy grasslands (in decreasing order of presence; Supplementary Table S1) and *Ranunculus repens* L., *P. trivialis* L. *perenne* and *Holcus lanatus* L. in semi-natural grasslands. The mean number of plant species did not differ between grassland types. However, the twenty dairy grasslands together (gamma diversity; Whittaker, 1960) comprised less plant species than the twenty semi-natural grasslands: 34 versus 64, respectively (all sites: 72 species) (Fig. 1).

3.2. Soil biotic parameters

Microbial parameters did not differ between land use types (Table 2). Bacterial biomass tended to be lower ($P = 0.052$) in dairy grasslands.

Total soil faunal abundance and taxonomic richness were higher in dairy than in semi-natural grasslands (Table 3; Supplementary Table

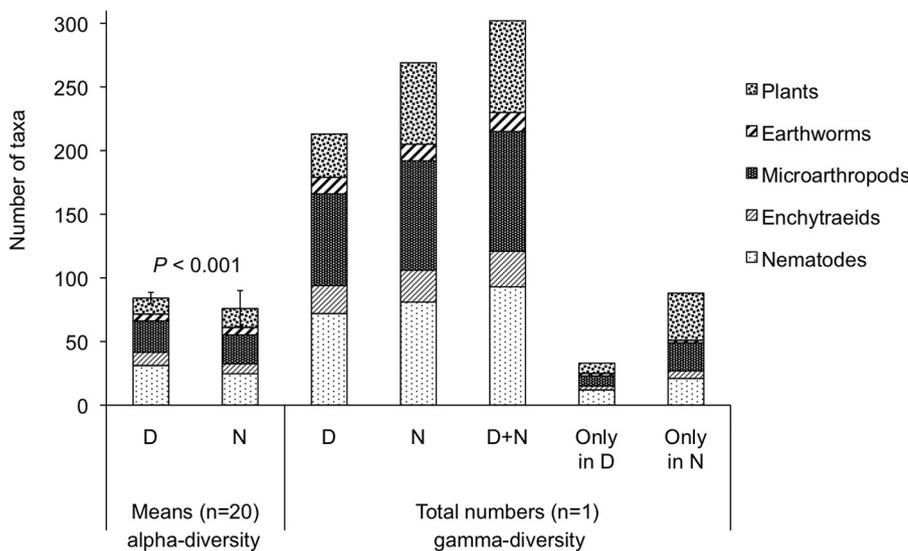


Fig. 1. Number of plant and soil faunal (nematode, enchytraeid, microarthropod, earthworm) taxa in dairy (“D”) and semi-natural (“N”) grasslands on peat. Error bars of taxa means represent the standard deviation for the five groups together (n = 20). Total numbers within all samples were used to calculate gamma diversity. The column “Only in D” represents the number of taxa present in dairy but not in semi-natural grasslands, and vice versa for “Only in N”.

Table 2

Soil microbial parameters of dairy (n = 20) and semi-natural (n = 20) grasslands on peat (0–10 cm) (means, standard deviations, P-values).

Parameter	Unit	Dairy		Semi-natural		P-value ^a
		mean	s.d.	mean	s.d.	
Fungal biomass	µg C.g dry soil ⁻¹	65.8	19.4	76.6	49.2	0.365
Percentage of active fungi	% hyphal length	5.6	6.4	4.8	4.7	0.638
Bacterial biomass	µg C.g dry soil ⁻¹	238.3	75.8	302.0	120.1	0.052
Thymidine incorporation	pmol.(g.h) ⁻¹	62.3	27.5	63.5	48.4	0.318
Leucine incorporation	pmol.(g.h) ⁻¹	1895	456	1998	836	0.981
Fungi:bacteria ratio	g g ⁻¹	0.30	0.11	0.27	0.15	0.382
Metabolic quotient (qCO ₂)	µg C.µg C _{micr} ⁻¹ .week ⁻¹	0.65	0.27	0.57	0.17	0.532
Potential C mineralization ^b	µg C. (g soil w.k) ⁻¹	183	58	203	66	0.310
Potential N mineralization ^b	µg N. (g soil w.k) ⁻¹	27.9	10.0	30.0	12.6	0.881

^a Maximum P-values for differences after correction for high number of parameters (see Section Methods): 0.024 at α = 5% (significant difference); 0.056 at α = 10% (trend, italic).

^b At field moisture.

S2). Differences in abundance were mainly caused by nematodes, earthworms and microarthropods, and differences in taxonomic richness by nematodes and enchytraeids. The combined soil faunal abundance index correlated positively with soil fertility (P_{total}, nitrate, pH) and soil structure (soil crumbs, root density) (Tables 4 and 5). The total number of observed soil faunal taxa in this study (gamma diversity) was 230, of which 179 taxa (78%) were present in the dairy grasslands and 205 taxa (89%) in the semi-natural grasslands (Fig. 1). The soil faunal taxonomic richness did not correlate significantly with the number of plant species.

Nematodes were more abundant in dairy than in semi-natural grasslands (Table 3) and correlated positively with soil abiotic parameters, especially nitrate (Table 5). No difference between the land use types was found in maturity and structure indices (Supplementary Table S2). The enrichment index was higher in dairy grasslands (P = 0.016), whereas the channel index tended to be lower (P = 0.046). In dairy grasslands, the proportions of bacterivorous and predatory nematodes were higher than in semi-natural grasslands,

Table 3

Soil faunal abundance and taxonomic richness of dairy (n = 20) and semi-natural (n = 20) grasslands on peat (means, standard deviations, P-values). Data on trophic, functional and taxonomic groups in Supplementary Table S2.

Parameter	Unit	Dairy		Semi-natural		P-value ^a
		mean	s.d.	mean	s.d.	
Number of soil faunal taxa	n taxa	71	4	61	12	< 0.001
<i>Nematodes</i>						
Abundance	n 100 g ⁻¹	8597	2267	6221	2803	0.005
Taxonomic richness	n taxa	31.2	2.8	24.7	6.1	< 0.001
<i>Enchytraeids</i>						
Abundance	n m ⁻²	31642	9967	37354	10841	0.091
Taxonomic richness	n taxa	10.3	2.1	7.9	3.0	0.007
<i>Earthworms</i>						
Abundance	n m ⁻²	587	318	270	247	0.001
Taxonomic richness	n taxa	5.4	1.9	5.9	2.9	0.598
<i>Microarthropods</i>						
Abundance	n m ⁻²	81157	33830	42944	33282	< 0.001
Taxonomic richness	n taxa	24.7	3.0	22.6	4.5	0.092

^a Maximum P-values for differences after correction for high number of parameters (see Section Methods): 0.024 at α = 5% (significant difference, bold).

whereas the proportion of herbivorous nematodes was lower. The abundance of bacterivorous nematodes was positively correlated with pH (r = 0.69), nitrate (r = 0.65) and soil crumbs (r = 0.74) (all at P < 0.001).

Enchytraeid abundance did not differ between grassland types (Table 3) but *Fridericia* species were more abundant in dairy grasslands, where they were dominant (Supplementary Table S2). Consequently, enchytraeid mean body weight was higher in dairy grasslands. The abundance of *Fridericia* enchytraeids was positively correlated with soil pH (r = 0.68; P < 0.001).

Earthworms were c. twice as abundant in dairy than in semi-natural grasslands (Table 3), with a higher proportion of juveniles (Supplementary Table S2). Earthworm density correlated positively with soil macropores and pH (Table 5). The proportions of epigeic and endogeic earthworms were similar in both grassland types. No anecic earthworms were found.

Microarthropods were nearly twice as abundant in dairy than in semi-natural grasslands (Table 3) and their density correlated positively with nitrate, P_{total}, root density and soil crumbs (Table 5). Fungivorous microarthropods were dominant in both grassland types and more abundant in dairy grasslands (Supplementary Table S2). In dairy grasslands, the proportion of omnivorous microarthropods and of

Table 4
Soil abiotic parameters of dairy (n = 20) and semi-natural (n = 20) grasslands on peat (means, standard deviations, P-values). Additional parameters in Supplementary Table S3.

Parameter	Unit	Dairy		Semi-natural		P-value ^a
		mean	s.d.	mean	s.d.	
<i>Soil physical parameters</i>						
Crumbs (0–10 cm)	%	79	15	46	27	< 0.001
Roots (at 10 cm depth)	n 400 cm ⁻²	306	76	153	102	< 0.001
Macropores (at 10 cm depth)	n 400 cm ⁻²	5.7	4.9	2.4	2.1	0.010
Water infiltration rate	mm min ⁻¹	31.6	32.0	6.2	7.9	0.001
Bulk density	g cm ⁻³	0.54	0.09	0.49	0.17	0.273
Field water content	Vol. %	51.7	5.0	57.8	9.9	0.019
<i>Soil chemical parameters</i>						
Clay (< 2 μm)	g 100 g soil ⁻¹	23.2	4.2	19.1	5.3	0.009
Organic matter (SOM)	g 100 g soil ⁻¹	43.8	8.8	40.3	10.6	0.197
pH _{KCl}	–	4.8	0.3	4.4	0.5	0.002
C _{total}	g 100 g soil ⁻¹	22.4	4.5	20.9	5.9	0.355
Hot water extractable C	μg C g soil ⁻¹	9309	1852	7282	1258	< 0.001
Water soluble C	μg C g soil ⁻¹	438	89	467	281	0.704
N _{total}	g 100 g soil ⁻¹	2.01	0.46	1.77	0.39	0.073
Potentially mineralizable N	μg N g soil ⁻¹	465	98	334	76	< 0.001
P _{total}	g 100 g soil ⁻¹	0.73	0.11	0.53	0.13	< 0.001
Plant available P (P _{AL})	mg P ₂ O ₅ 100 g soil ⁻¹	52.7	22.7	26.4	16.2	< 0.001

^a Maximum P-values for differences after correction for high number of parameters (see Section Methods): 0.024 at α = 5% (significant difference, **bold**).

fungivorous grazers, but not browsers, was higher. In contrast, the proportion of herbivorous grazers, but not browsers, was lower.

3.3. Soil abiotic parameters

Dairy grasslands differed from semi-natural grasslands in soil structure, with more crumbs and higher numbers of macropores and roots, and a higher water infiltration rate (Table 4). Bulk density did not differ, but soil water content was lower in dairy grasslands. At pF 2, soil water and air contents did not differ between grassland types (Supplementary Table S3). Penetration resistance was higher (significant below 10 cm depth) in dairy grasslands, as was load-bearing capacity. Dairy grasslands had slightly higher clay contents than semi-natural grasslands. Soil pH, HWC, potentially mineralizable N, P_{total} and P_{AL} were higher in dairy grasslands. No differences were found for SOM, C_{total}, N_{total}, C:N ratio or WSC.

Table 5
Significant Pearson correlations (r; n = 40) between the abundance of nematodes, enchytraeids, microarthropods and earthworms and soil abiotic parameters in grasslands on peat.

Soil abiotic parameter	Combined abundance index	Abundance of soil faunal group			
		Nematodes	Enchytraeids	Microarthropods	Earthworms
P _{total}	0.67 ***	0.49 **	n.s.	0.60 ***	0.49 **
Nitrate	0.72 ***	0.68 ***	n.s.	0.73 ***	0.47 **
pH _{KCl}	0.63 ***	0.56 ***	n.s.	0.37 *	0.64 ***
Field water content	-0.41 **	n.s.	n.s.	-0.43 **	-0.33 *
Crumbs	0.63 ***	0.57 ***	n.s.	0.62 ***	0.57 ***
Roots	0.53 ***	0.54 ***	-0.34 *	0.71 ***	0.46 **
Macropores	0.44 **	n.s.	-0.40 *	0.52 ***	0.70 ***

* P < 0.05.
** P < 0.01.
*** P < 0.001.

3.4. Ecosystem services

SEM yielded four models that significantly explained variance in the parameters (i) combined index of soil taxonomic richness (ecosystem service “maintenance of biodiversity”), (ii) potential C mineralization (“climate regulation”), (iii) water infiltration (“water regulation”), and (iv) potential N mineralization (“grass production”) (Fig. 2).

The combined index of soil taxonomic richness was positively correlated with soil pH and root density, and root density was linked with percentage of grass cover and soil N_{total} (Fig. 2a). Potential C mineralization was positively correlated with soil water content and weakly, but significantly, to HWC (Fig. 2b). Higher HWC was found at higher C_{total} and root density. Water infiltration was positively correlated with number of macropores and percentage of soil crumbs, while macropores correlated with earthworm abundance, and soil crumbs with root density and soil pH (Fig. 2c). Potential N mineralization was negatively correlated with bacterial biomass but positively with thymidine incorporation, and was indirectly correlated with the amount of potentially mineralizable N (Fig. 2d).

4. Discussion and conclusions

4.1. Ecosystem service “maintenance of biodiversity”

The average abundance and taxonomic richness of soil biota were higher in dairy grasslands, but the gamma diversity in this land use was lower than in semi-natural grasslands (Fig. 1). Our hypothesis did not include this effect of scale and had therefore to be partly rejected.

At the scale of grassland, the variation in soil faunal taxonomic richness between sites was explained by soil pH and root density (Fig. 2a). Taxonomic richness correlated positively with soil crumbliness and nutrient concentrations. A positive influence of nutrient levels is in line with studies of grasslands on sand and clay soils (Mulder and Elser, 2009; Van der Wal et al., 2009). Within the individual groups – particularly nematodes, earthworms and microarthropods – trophic or life stage distributions confirm an overall positive sensitivity to nutrient levels, pH, input of young organic matter and soil temperature. First, the higher nematode counts in dairy grasslands were due to a higher number and proportion of bacterial feeders, correlating with soil fertility parameters such as pH, P_{AL} and nitrate concentrations (r = 0.69, 0.60 and 0.65, respectively; P < 0.001). This may be explained by a higher input of easily decomposable organic matter to the soil via manure and primary production (plant residues, root exudates) in dairy grasslands (Biederman et al., 2008; Yeates, 1987). Second, the abundance of earthworms, particularly of juveniles, was higher in dairy grasslands. This is likely to be related to the combination of higher soil pH (Curry, 2004), higher input of organic matter via primary production and manure (Bouché, 1977; Hansen and Engelstad, 1999) and drier (thus also warmer) soil conditions during the winter season (Plum and Filser, 2005; Timmerman et al., 2006) in those grasslands. Especially

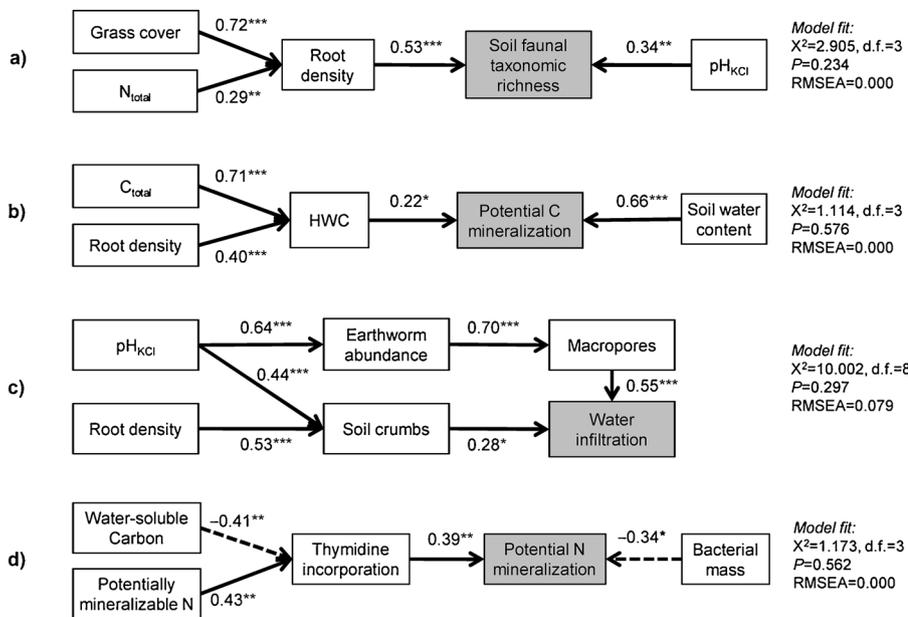


Fig. 2. Structural equation models based on data from 40 grasslands on peat for: a) Soil faunal taxonomic richness (combined index), b) Potential C mineralization, c) Water infiltration, d) Potential N mineralization. Arrows represent significant relationships (continuous: positive; dashed: negative). Numbers next to the arrows are path coefficients; stars indicate their significance level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). An adequate model fit is indicated by non-significant Chi²-test ($P > 0.050$) and low RMSEA (< 0.080).

the higher proportion of juveniles in dairy grasslands (sampled in April) indicate more favorable soil conditions: earthworm densities increase when overwintered cocoons start to hatch at increasing temperature in spring (Edwards and Bohlen, 1996). Lastly, the higher numbers of microarthropods in dairy grasslands with more predators and less herbivores indicate a more dynamic environment and a richer diet. Within grassland systems, different studies showed increased microarthropod densities with improved soil fertility and plant productivity (Cole et al., 2005; King and Hutchinson, 1980). Thus, in our case, well-drained and well-structured dairy grassland soils supported a more abundant and diverse community of soil biota than semi-natural grassland soils due to higher root density, pH, nutrient input and probably also higher soil temperatures in winter and spring.

In contrast to the above, the diversity across sampling sites (gamma diversity) was lower in dairy grasslands (Fig. 1). This indicates that the botanical and soil faunal taxonomic composition was quite homogenous across dairy grasslands, and more diverse across semi-natural grasslands. This could well be related to a lower diversity in land management across dairy grasslands, as reflected in lower standard deviations in most abiotic soil parameters (Tables 1 and 4). These findings have implications for nature conservation in managed peat areas at field and landscape scale. First, the trend in modern agriculture towards low inter-farm diversity (Swift et al., 2004) should be reversed to promote diversification of agroecosystems and nature-inclusive agriculture (Erisman et al., 2016). Second, the lower soil faunal diversity of individual semi-natural grasslands may imply that with the current management, many (semi-)natural grasslands are needed to increase the total nature value. Finally, our results emphasize the importance of considering the spatial scale when evaluating ecological observations (Ettema and Wardle, 2002).

In relation to the ecosystem service “maintenance of biodiversity”, we conclude that soil faunal abundance and diversity were greater in dairy grasslands due to higher input of fresh, nutrient-rich organic matter and drier soil conditions in spring. However, the gamma diversity (at land use scale) was lower in dairy grasslands due to a lower inter-farm diversity.

4.2. Ecosystem service “climate regulation”: CO₂ emission

Potential C mineralization is a measure of the decomposition of organic matter by heterotrophic microorganisms in soil (Haynes, 2005). Our CO₂ measurements during 6-week laboratory incubations of field

moist soil therefore indicated field C mineralization and CO₂ emission.

Contrary to our hypothesis, the results do not indicate differences in potential C mineralization or in microbial activity between dairy and semi-natural grassland soils. However, other soil properties that may influence the C mineralization rates such as soil water content, HWC (a labile C pool) and pH (Ghani et al., 2003; Wang et al., 2003) were influenced by grassland type. The SEM model explaining potential C mineralization showed a combined dependence on HWC and soil water content (Fig. 2b). Surprisingly, the effect of soil moisture was positive, indicating that mineralization may have been limited by dry topsoil in the dairy grasslands, compared to the wetter semi-natural grasslands. Semi-natural grassland soils were wetter but still had sufficient soil air volume (> 10%) for aerobic processes (Da Silva et al., 1994). There is evidence that in peat grasslands, soil respiration can be limited by the lack of air at high soil water levels, but also by drought in situations of deep drainage (Berglund and Berglund, 2011).

Although potential C mineralization was similar in both grassland types, correlations with other soil parameters in the separate subsets show interesting differences. In both cases, the limitation by drought was dominant (Supplementary Table S4). In dairy grasslands, potential C mineralization was also correlated with HWC and clay percentage. HWC itself correlated with C_{total} , N_{total} , potentially mineralizable N and root density (Supplementary Table S5). Therefore, in dairy grasslands, the mineralized C seemed to originate principally from a pool of labile organic substrate (reflected by HWC) from relatively young organic matter: livestock manure, grass residues and rhizodeposition (Ghani et al., 2003; Haynes, 2005). In semi-natural grasslands, however, a strong correlation of potential C mineralization was found with WSC and microbial biomass. WSC is a labile C fraction in soil that consists of both relatively resistant humic acids formed by microbial degradation, and readily degradable carbohydrates which are key substrates for microbial activity (Haynes, 2005). Being partly a substrate for potential C mineralization, the WSC pool in semi-natural grasslands was relatively small (Tables 2 and 4: only c. twice the amount of the C mineralized per week). The positive correlation therefore indicates that WSC was limiting C mineralization. In this situation, a fast replenishment of the WSC pool has to be realized by microbial activity and physical-chemical processes producing WSC from soil C_{total} and plant residues (Haynes, 2005). In our data set, WSC indeed correlated positively with soil water content, fungal biomass and C_{total} (Supplementary Table S5). Thus, in semi-natural grasslands, potential C mineralization appeared to be determined by highly degradable organic substrate (WSC), which

in turn was dependent on soil fungi and soil water for replenishment from C_{total} . Finally, the higher nematode enrichment index in dairy grasslands and the higher nematode channel index in semi-natural grasslands support the observation that C mineralization was more bacterial driven in dairy grasslands and more fungal driven in semi-natural grasslands (Ferris et al., 2001).

Our measurements were carried out in grassland types differing in drainage intensity. The lack of difference in potential C mineralization is surprising, because drainage and an oxic topsoil is seen as the main reason for progressive peat decomposition (Kasimir-Klemedtsson et al., 1997; Kluge et al., 2008; Krüger et al., 2015; Schothorst, 1977). However, we measured the microbial parameters in the 0–10 cm layer only, in line with standard methods for ecological research in grassland soils (Bloem et al., 2006; Rutgers et al., 2009; Stone et al., 2016; Van Eekeren et al., 2010). Although CO_2 release in peat soils typically decreases with depth (Kluge et al., 2008), C mineralization can rapidly increase following exposure of the anaerobic subsoil to oxic conditions (Brouns et al., 2014; Chow et al., 2006). Potential C mineralization in samples from the topsoil is not indicative of CO_2 release from deep peat soils, especially with fluctuating ground water level.

In relation to the ecosystem service “climate regulation”, we conclude that the rate of C mineralization in the topsoil was not influenced by land management, but was limited by drought in both dairy and semi-natural grasslands. In addition, C mineralization seemed to involve different C sources and microbial groups per grassland type: in dairy grasslands, potential C mineralization correlated with HWC originating from relatively young organic matter, whereas in semi-natural grasslands it correlated with WSC, which was dependent on soil fungi and soil water for replenishment from C_{total} .

4.3. Ecosystem service “water regulation”: water infiltration

Our measurements do not support the hypothesis that dairy grasslands have low water infiltration rates due to inferior soil structure caused by farming activities. On the contrary, dairy grasslands were drier and had a higher percentage of crumb structures, more macropores, more roots and a higher water infiltration rate than semi-natural grasslands. The lower soil moisture content is probably a direct effect of more intensive drainage combined with higher evapotranspiration in more productive grasslands, and also explains the higher load bearing capacity and penetration resistance (Schothorst, 1982). Water infiltration appeared to be determined by soil macroporosity and crumbliness, and indirectly by parameters related to biological activity (earthworm abundance, root density) and pH (Fig. 2c). Root density was linked with percentage of grass cover and soil N_{total} . Causalities between these parameters are well documented, partly also for peat soils (Bouché and Al-Addan, 1997; Curry, 2004; Dettmann et al., 2014; Holden, 2005; Van Eekeren et al., 2009b). The differences in soil structure, soil biota, root density and pH between dairy and semi-natural grasslands are therefore clear explanations for the different water infiltration rates.

In view of future climate change scenarios (KNMI, 2014), the water infiltration capacity of soils is important for flood prevention, because water storage in the soil reduces peak loads of drainage water in ditches and rivers. Our results show that the soil properties of semi-natural grasslands lead to a limited water infiltration rate compared to dairy grasslands, and that these soil properties are inherently linked with the management of these grasslands: high water levels and low organic matter inputs resulting in low soil biological activity. Ways to improve water infiltration capacity in semi-natural grasslands (i.e. control of soil acidity, more manure for earthworms and higher grass cover for root density) are therefore limited and may compromise the primary land use and management objectives of these areas.

In relation to the ecosystem service “water regulation”, we conclude that soil biological activity, including plant roots, plays a key role. In semi-natural grasslands, the biological activity and water infiltration rates were lower than in dairy grasslands.

4.4. Ecosystem service “grass production”: soil fertility

The contribution of the peat soil to the ecosystem service “grass production” was assessed from abiotic (pH, nutrient concentrations, soil structure) and biotic soil parameters (potential N mineralization) (Haynes, 2005; Van Eekeren et al., 2010). As expected, dairy grassland soils had higher pH and higher concentrations of plant available nutrients than semi-natural grasslands. However, contrary to our hypothesis, the potential N mineralization, an indicator of the ability of soils to supply crops with mineral N (Haynes, 2005), was similar in both grassland types.

The higher pH in dairy grasslands may be the result of differences in H^+ production (cation uptake by plants, SOM accumulation) and consumption (decomposition and mineralization of SOM) (Bolan and Hedley, 2003; De Klein et al., 1997). Moreover, pH may have been influenced by liming in the past as part of standard practice. Similarly, the observed differences in soil P and N between grassland types (Table 4) can be attributed to contrasting management types. It is known that P accumulates in dairy systems due to long term use of animal manure because of its relatively high P:N ratio (Whalen and Chang, 2001). In addition to higher pH and nutrient availability, dairy grassland soils were more crumbly and had higher root densities than semi-natural grassland soils, presumably due to a combination of drier conditions during winter, higher biological activity and a higher grass cover.

Potential N mineralization did not significantly differ between grassland types and was three times higher than in grasslands on sandy soils (Van Eekeren et al., 2009a). These high values can be explained by the high SOM, N_{total} and potentially mineralizable N contents of peat soils. The ratio of potentially mineralizable N to potential N mineralization in peat (10–15) was higher than in sandy soils (7). On peat, the differences in potentially mineralizable N between dairy and semi-natural grasslands did not result in diverging potential N mineralization rates. Apparently, the amount of mineralizable N did not limit mineralization rate. Potential N mineralization is the net result of ‘gross’ mineralization of labile N minus N immobilization into microbial biomass and N loss by denitrification (Haynes, 2005; Hodge et al., 2000). In the SEM, potential N mineralization was positively correlated with bacterial growth measured by thymidine incorporation, and negatively with bacterial biomass (Fig. 2d). In this model, bacterial growth can be a reflection of the ‘gross’ N mineralization, and bacterial biomass a reflection of N immobilization. Microbial activity and N mineralization are positively influenced by microbivores such as protozoa and nematodes (Bloem et al., 1994; Bouwman et al., 1994). In our data, however, there was no significant correlation between thymidine incorporation and bacterivorous nematodes. Instead, thymidine incorporation was determined by WSC (negative correlation) and potentially mineralizable N (positive correlation) (Fig. 2d). Substitution of WSC and potentially mineralizable N by soil C:N ratio in this model did not lead to a significant fit, which indicates sensitivity of bacterial growth to the labile fractions rather than to the total pools of soil C and N. The importance of N immobilization in our peat soils is indicated by i) the negative correlation of microbial biomass and potential N mineralization (Fig. 2d), ii) the lack of direct correlation between the amount of mineralizable N and N mineralization (Fig. 2d) and iii) the absence of correlation between potential N mineralization and potential C mineralization ($r = 0.02$) (Haynes, 2005).

Concerning the ecosystem service “grass production”, we conclude that dairy grasslands had higher pH, nutrient concentrations and better soil structure, as expected. However, potential N mineralization rate was not affected by land management but was controlled by variation in bacterial biomass apparently indicating N immobilization, and by bacterial growth that depended on the amounts of labile C and N in soil.

5. Perspectives and recommendations

Drained peat soils worldwide contribute 6% to the anthropogenic CO₂ emission, which is disproportional to their relatively small surface (0.3% of the land area) (Joosten, 2011). Although CO₂ emission and contribution to climate change are the major concerns for these soils, we examined effects of land use in a broader context, including maintenance of biodiversity, water regulation and potential for agricultural production. Our study results in the following recommendations for land use policy and land management of peat grasslands.

5.1. Biodiversity

Spatial scale is of crucial importance in maintaining biodiversity and considering biodiversity management strategies. Especially in dairy grasslands, diversification in management between sites and farms may increase biodiversity at larger geographical scale. Similarly, diversity in types and management of (semi-)natural grasslands is needed to keep a high above and belowground biodiversity at landscape scale. Diversification may be found in drainage management, type of vegetation, nutrient management and use of grazing livestock.

5.2. Climate regulation

For dairy grasslands, management should focus on sufficient input of organic matter to compensate for topsoil decomposition, and on minimal peat decomposition in subsoil for example by water management with submerged tile drains. For semi-natural grasslands, management should focus on reducing peat decomposition by raising ground water levels, and on stimulating C accumulation in the soil. This may imply changes in vegetation type and can negatively affect biodiversity conservation objectives, for example concerning meadow birds.

5.3. Water regulation

Management of dairy grasslands should focus on maintaining a high water regulation capacity by sustaining soil biological activity (earthworms, rooting) through sufficient organic matter input and control of soil pH. In semi-natural grasslands, however, options to improve water infiltration (i.e. increasing soil biological activity with organic matter input, control of soil pH and drainage during the wet season) are limited. Water regulation strategies in these areas should therefore be based on fluctuating (and high) surface water levels and appropriate vegetation types.

5.4. Grass production

N supply from soil to grass appears to depend mainly on mineralization of young organic matter. Input of organic N to the soil (crop residues, manure) should therefore be equal to net mineralization.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.apsoil.2017.12.011>

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